# The Genus *Crocus* (Liliiflorae, Iridaceae): Lifecycle, Morphology, Phenotypic Characteristics, and Taxonomical Relevant Parameters

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**Abstract:** The genus *Crocus* L. was studied by the authors for more than 30 years in nature as well as in cultivation. Since 1982 when the last review of the genus was published by Brian Mathew many new taxa were found and work dealing with special parameters of *Crocus*, like the Calcium-oxalate crystals in the corm tunics, were published. Introducing molecular-systematic analyses to the genus brought a completely new understanding of *Crocus* that presents itself now far away from being small and easy-structured. This work was initiated by the idea that a detailed study accompanied by drawings and photographs is necessary to widen and sharpen the view for the important details of the genus. Therefore we look at the life-cycle of the plants as well as at important morphological and phenotypical characteristics of *Crocus*. Especially important to us is the explained determination of relevant taxonomical parameters which are necessary for a mistake-free identification of the rapidly increasing numbers of discovered species and for the creation of determination keys.

**Zusammenfassung:** Die Gattung *Crocus* wird seit mehr als 30 Jahren von den Autoren sowohl in der Natur als auch in Kultur studiert. Seit 1982, dem Erscheinungsjahr der letzten Revision der Gattung durch Brian Mathew, wurden viele neue Arten entdeckt und Arbeiten über spezielle Themen von *Crocus*, wie zum Beispiel die Calciumoxalat Kristalle in den Knollenhüllen, veröffentlicht. Seit genetische Analysen zur Erkennung der verwandtschaftlichen Beziehungen in der Gattung verwendet werden, konnte auch ein neues Bild der Gattung gezeichnet werden, die weit davon entfernt ist, klein und einfach strukturiert zu sein. Die vorliegende Arbeit wurde durch die Idee geboren, dass eine detaillierte Studie, die durch Zeichnungen und Fotos begleitet wird, notwendig ist um den Blick für die wichtigen Details in der Gattung zu weiten und zu schärfen. Aus diesem Grunde blicken wir auf den Lebenszyklus der Pflanzen aber auch auf die wesentlichen morphologischen und phänotypischen Charakteristika von *Crocus*. Besonders wichtig für uns ist die erklärte Feststellung von taxonomisch wichtigen Parametern, die für eine fehlerfreie Identifizierung der rasch ansteigenden Zahl von neuen Arten und für die Erstellung von Bestimmungsschlüsseln notwendig ist.

**Key words:** *Crocus*, life-cycle, morphology, phenotypic characteristics, morphometry, taxonomical relevant parameter.

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### INTRODUCTION

The genus *Crocus* has been studied by us since 1983. Until today hundreds of wild populations were seen in the field, investigated and the results published (Kerndorff 1988, 1993, 1995). From this work it was clear that more systematic investigations of crocuses in their natural habitats are necessary (Kerndorff & Pasche 1994, 1996, 1997, 1998, 2003, 2004a, 2004b, 2006, 2011, 2012, and 2013; Pasche 1993, 1999) as well as molecular analyses to get more information on species relationships (Harpke et al., 2013). These were initiated in 1993 respectively 2006 and are continuing up today. During that period a great deal of

new information about the genus was accumulated and experience gathered by the authors. A real important progress was made since systematic molecular analyses came into the investigations. Those results gave us a new understanding of the whole genus but especially of section *Nudiscapus*.

One important aspect of the new situation is the necessary change of the more or less coarse sight on and assessment of morphological characteristics into a more detailed one. The achieved and rather detailed phylogenetic results require a new and adequately detailed sight, especially on the morphology and the phenotypic parameters of the species to recognize the often rather subtle but, as we know now, important differences.

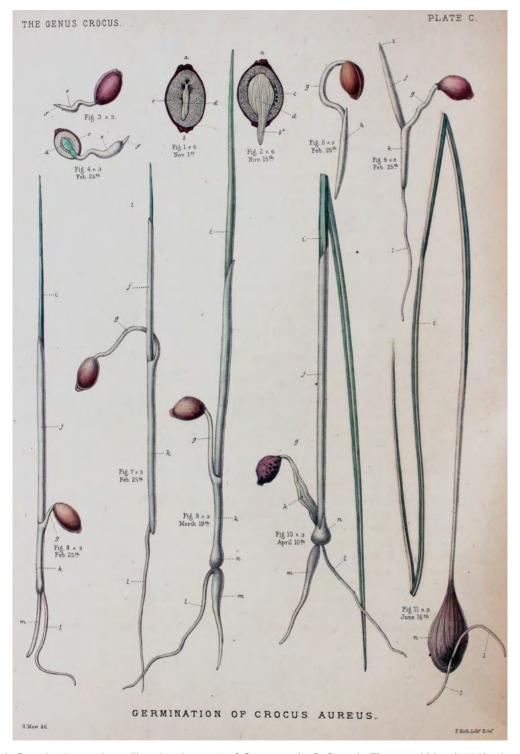


Fig. 1: Germination and seedling development of C. aureus (= C. flavus). (Extract of Maw (1886), altered.) **Explanatory notes:** 

- Fig. 1 (cross-section of dor-
- mant seed) a caruncle extremity
- b base (chalazal extremity)
- c endosperm
- d embryo
- Fig. 2 (first stage of germination)
- b x base of cotyledon
- c endosperm

- d enlarged apex of cotyledon absorbing the endosperm
- Fig. 3 & 4 (further stage of germination)

- c endosperm
  d enlarged apex of cotyledon
  e base of cotyledon further produced with primary root, protruding
- Fig. 5 (further stage)
- g cotyledon
- base of the cotyledon including the plumule
- Fig. 6 (further stage)

- g cotyledon k base of cotyledon j sheath of the first leaf, protruding at i
- Fig. 7-10 (further stages) g cotyledon
- first leaf
- sheath of the first leaf
- k base of cotyledon
- I primary root
- m an enlarged ephemeral root (= contractile root)
- n the young corm

### Fig. 11

n the young corm of the first season

The life-cycle of a crocus presents many different valuable facts for different species which can help to learn more about the genus and to distinguish species more easily. Morphological parameters are continuously varying and have to be measured in a statistically relevant number of specimens preferably in wild populations to receive representative information about their values. This will be dealt with in the chapter determination of taxonomical relevant parameters where also detailed advices are given how to measure continuously varying parameters of major interest.

### 1. THE LIFE-CYCLE OF A CROCUS

### 1.1 Germination, dormancy, and maturity

The life-cycle of a crocus begins with the germination of the seed and continues by various stages of seedling development in the first year and further development in the following years leading after 3-5 years to the mature plant. The autumn-flowering crocuses germinate generally from September to November; the vernal species at their flowering time in spring, dependent on climatic conditions and habitat which means actually from mid-winter into spring. Crocus seeds have prolonged germination ability and many seeds only germinate after another year or even more years dormant in the ground. The whole process of germination and seedling-development is perfectly drawn and explained by Maw (1886) in his monograph of the genus. As an example he shows the germination and development of Crocus aureus Sibth. & Smith (= C. flavus Weston) in its first year. To honour Maw's meticulous work and to make his informative drawing available for a larger audience we reproduce it here with minor alterations (Fig. 1).

In the first year the crocus produces only one leaf to create a corm which has a diameter of about 5-8 mm dependent on species. It is already covered by a thin tunic at that time, which is, of course, not yet useful for taxonomic differentiations. When the hotter and dryer times arrive every year the crocus has to go into dormancy. At that time all parts of the young and not even one year old crocus die away except the corm. After the first dormancy the corm normally "wakes up" for a new life-cycle when temperatures in the soil drop. This is indeed predominantly a matter of low temperatures in the soil and less of soil humidity. We proofed this when studying the root-development of crocuses. We investigated several flowering specimens of different autumn-flowering species in nature and found out, that in a vet dry soil after summer their corms had no roots due to lack of humidity. This means at the beginning of dormancy the corm has everything ready to produce quickly flowers without roots when temperatures are favourable. After the first season this picture changes and one has to distinguish between two cases of dormancies:

1. High-mountain crocuses seem to have, due to harsh environmental conditions, a prolonged dormancy as after summer nothing of the reawakened crocus appears above ground until next spring when conditions get favourable again. Meanwhile, predominantly in autumn, the crocus produces new roots and shoots of new leaves to be ready for the next season. If conditions allow, on warm days in spring when snow melts away and roots get sufficient water and nutri-

- ents the young crocus pushes up two or more leaves above ground for the upcoming season dependent on species.
- 2. Lowland crocuses e.g. on Mediterranean coasts have much more favourable conditions during winter and also produce leaf-shoots and new roots after dormancy. The main difference to case one is, that leaves appear already in fall and winter above ground when rains make the soil sufficiently wet. This is useful as there are reduced and weakened frost periods, no or negligible snow-covers but sufficient light for photo-synthesis for many weeks. On the other hand prolonged drier periods are frequent in these areas which force the crocus to take in its leaves with the first spell of heat which arrives in general much earlier than in the higher mountains.

The behaviours of growing crocuses in both scenarios are repeated season for season until after 3-5 years the crocus normally reaches its maturity. However, there is one major alteration in the life-cycle of these years. From the second season onwards the new corm is built on top of the old one by consuming the old one totally until next dormancy. This means that from the second season onwards the whole plant renews itself every year. This is a great advantage for the life of a crocus. Even when some old corms are somehow injured, due to the production of the new one the whole plant can recover perfectly for the next season. Even a greater advantage comes from the kind of leaf-growth. Crocus leaves have a so-called intercalary growth, which simply means that the growing point is at the base of the leaf rather than at the tip. In case the leaves are eaten by grazing goats they can regrow leaf-mass to continue photosynthesis for the building of the new corm, which in this case gets a bit smaller.

Finally also the life-cycle for mature crocuses changes again depending on the flowering-time. The following cases can be distinguished:

- 1. High mountain crocuses flowering in autumn
  - All high mountain crocuses flowering in autumn do this without leaves above ground. Because the leaves develop after flowering-time they are called hysteranthous. For these crocuses leaves would be useless because the expected high and long-lasting snow-covers prevent photosynthesis for a longer period. Instead, the flowers are produced quickly, often several in succession, before situations get harmful. In case of fertilization the flowers wither quickly away but the capsules containing the growing seeds develop slowly underground using the accumulated "energy" of the new corm. In the following spring when conditions get dry and warm again leaves and pedicels grow quickly. The capsule is then pushed significantly above ground by the pedicel, splits open and sets the ripe seeds free. There are, however, exceptions of this behaviour by species of series Orientales which ripen their capsules in the underground. After seeddispersal and corm-ripeness the leaves retract and the crocus goes to dormancy again.
- 2. High mountain crocuses flowering in spring

After a short summer when dormancy ends with cold days coming up, the crocus starts to produce leaf- and flower-shoots but all stay in the ground. With increasing wetness, also roots start to grow. At the end of winter or when conditions get amenable for plant-life again the crocus is able to

develop flowers within hours, accompanied by more or less strong leaf-development in the following weeks. Leaves and flowers developing at the same time are called synanthous. There is also the possibility to produce flowers in succession, likewise the autumn-flowering species. This is in general a very useful mechanism for survival. A grazed flower can almost immediately be substituted by new ones. In case of fertilization, the flowers quickly shrivel away and capsule and seeds grow fast in the short summer. The pedicel pushes, like in the autumn-flowering ones, the capsule above ground so that the ripe seeds can be dispersed in dry weather. Before the crocus goes into dormancy again the new corm matures on top of the old one.

### 3. "Lowland" crocuses flowering in autumn

The Mediterranean climate-zone all around the Mediterranean coasts extend from sea-level to a maximum elevation of 1000-1200 m. In this environment a large number of species can be found. The prolonged dormancy period in these areas is compensated by the vegetative period during winter. After dormancy the crocus starts to flower from October to December by pushing up the "ready-to-go" flower-shoots. Most of the crocuses in these areas show a parallel (synanthous) leaf-development. This is useful as the new corm ripens faster and is usually matured when early hot weather spells force the crocus to retract leaves very quickly in terms of only a few days. For this reason, in some species the leaf-development above ground occurs even before the flower is built.

### 4. "Lowland" crocuses flowering in spring

The spring-flowering season in the Mediterranean starts already in winter and lasts approximately from January to March or April rarely to May. However, in some cases it is not really separable from the autumn-flowering ones. Examples for this behaviour are species like *C. cambessedesii* and *C. laevigatus* which can flower from autumn to spring. The spring crocuses of these areas generally develop their leaves above ground before or with the flowers. Their life-cycle is, therefore, not very different from the autumn-flowering ones, except for their flowering-time and, consequently, the necessity to ripen the seeds in a shorter period.

### 1.2 Contractile Roots

The seed normally germinates near the surface but the adult corm only can be found between 5 to 15 cm deep (in C.flavus sometimes even deeper). There was no explanation for Maw to this effect although some research concerning this subject started already six years before he completed his monograph (DE VRIES, 1880) but without significant results at that time. Maw believed in "some power" of descending the corm deeper into the ground..."it must be viewed as one of many self-protective phenomena in plant-life, the modus operandi of which we do not understand". More research on this effect followed by RIMBACH between 1898 and 1929 without final results (Rimbach 1898). In the last century, more light was brought into this field by several workers, especially by Pütz (1991 to 1998) who proved the pulling force of the so-called contractile roots and measured it for the first time. The phenomenon as a whole consists of different complex mechanisms in different plant families as well as of the dicotyledons and is still not solved for several aspects.

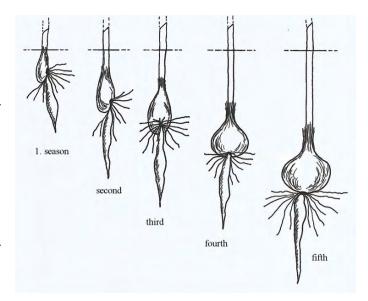


Fig. 2: Down-pull and turn of corm by contractile roots.

However, as can be seen on Maw's drawing (Fig. 1), the young crocus corm has, besides string-like primary roots (l, in Fig. 1), a large "ephemeral" root (in the sense of short-lived) which seemed to him ... "an inherited recurrence of a constant feature of the later stages of germination" (m in Fig. 1).

These contractile roots have the ability to move parts of the plants deeper into the soil by contracting themselves. This characteristic is very fundamental for the survival of seedlings in the geophytic monocotyledons and known for several genera of the Iridaceae and Amaryllidaceae. The question is how do they do this? As experiments show a) radial expansion and shortening have no causal connection and b) the shortening is not a growing-process of the cell wall. According to the present knowledge there are different kinds of contractile roots with different processes and purposes. For the best investigated cases (type Iridaceae, Crocus) the following hypothesis of the "pulling-effect" is most probable. The bark-cells of the root are expanded longitudinally during the stretching process in which a specific wall-elasticity of this expansion is memorized similar to a rubber-band. The turgor is active as a contra-pressure. However, still many details in this astonishing but difficult to observe process have to be investigated.

Another, yet little known effect connected with contractile roots in *Crocus* has to be mentioned here. It is confined to species, which renew their corms on top of the old one as it is the case in *Crocus*. Such corms are called orthotropic rhizomecorms. Surprisingly, these often show a turning of their individuals during down-pull (Fig. 2). In *Crocus* the pulling-depth is approximately 1-1.5 cm per growing season.

When the corm has reached the "physiological optimum depth" no contractile roots are produced any more. Several exogenous factors were proofed to induce the "pulling-activity".

- 1. The temperature gradient in the soil (amplitude) is dependent on the depth. The deeper the corm is in the soil the flatter the amplitude of temperatures for it. The shallower the corm is positioned the higher differences of temperatures are in soil between day and night. High differences in temperatures cause contractile root growth. This is very significant and can be also a memory effect of the past year growth.
- 2. After dormancy, the crocus produces already cataphylls in a rudimentary state, which stay in the soil for a while. In case of young (shallow) corms light can fall on these and signalizes to the plant that it is too shallow in the soil, which induces contractile root-growth. As a consequence no contractile roots are induced in the dark.

Finally, the root-growth of a corm before it has reached its optimum depth is vertical to radial downwards from the corm. In its optimum depth it is horizontally away from the corm.

### 1.3 Pollination and seed growth

Pollination and fertilization of a crocus consists of complex mechanisms, which only can be presented briefly here. In any case it is the prerequisite for the growth and ripening of seeds and closes the life-cycle of the crocus. The pollination is generally accomplished by insects (e.g., bees, flies, beetles) meaning crocuses are entomophilic or, in general, zoophilic. The most important characteristics of zoophilic plants are, they are angiosperms, have hermaphrodite flowers, striking colours, strong fragrance, pollen or nectar as nourishment to offer, strongly marked surfaces of pollen and high amounts of pollen cement. However, in crocus mainly little or normal amounts of pollen cement seem to occur. Also strongly marked surfaces of the pollen do not occur. They are either inaperturate or weakly to sometimes strongly spiraperturate (Fig. 20).

The whole process starts with the opening of the flower. An important internal factor for the display of the flower is an increase of the turgor accomplished by an expansion of the cell wall. Loss of turgor e.g. in case of senescence leads to a permanent closure of the flower. The role of hormones in this process is contradictory discussed in literature and cannot be dealt with here. In any case the opening of the flower is controlled by external factors. For most spring-flowering crocuses the rise of temperatures above approximately 15 °C induces the opening of the flower. With some crocuses the intensity of light seems to play an evenly important role. This we could observe for species on higher mountains which open already at air temperatures below 10 °C when they get light enough and winds are not too strong. The opening and closure of the flowers is accomplished by the same mechanisms and depends on an endogen rhythm. This is valid for all crocuses except for C. cartwrightianus and C. tournefortii whose flowers do not close anymore once they opened up. These cell-physiological and especially genetic backgrounds for flower-opening are rather complex and yet little known.

Once the flower is open and external conditions are favorable and remain for a while, like sunny and dry weather, the pollen sac (theca) with the pollen ripens quickly. The theca then opens mostly longitudinally by a special mechanism of cohesion and releases the pollen, which is then spread by insects from flower to flower.

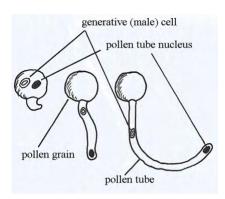


Fig. 3: Growth of pollen tube.

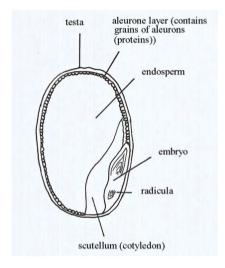


Fig. 4: Cross-section of dormant seed.

Pollination takes place when the (male) pollen is transferred to the (female) styles. The microspore starts a cell division inside the pollen wall which results in a generative cell and a vegetative cell (spermatozoids). Now the pollen tube starts to grow (Fig. 3) in direction of the synergids (help cells). The vegetative (pollen tube nucleus) as well as the generative cell moves into the pollen tube. Then the generative cell splits up into two sperm cells. After the pollen tube has reached a synergid the two sperm cells are released in the vicinity of the synergids (incompatible pollen is impeded to grow). One fuses with the oosphere the other one with the secondary nucleus of which the endosperm is built (double fertilization). The latter one functions later as storage tissue in the seeds. From the fertilized oospere the plant embryo develops inside the seed (Fig. 4). The ripening process of the crocus seeds lasts about 3-5 months, depending on species and climatic conditions.

Crocuses have to be cross-fertilized (allogamy) by genetically dissimilar individuals of the same species. This has the advantage of recombination of variable genetic material so that crocus populations show mostly the known great variation of individuals in a population. Another positive effect of allogamy is the greater adaptive potential compared to autogamic species.

# C. angustifolius

### subglobose

C. abantensis, C. ancyrensis, C. gargaricus, C. lazicus Boiss., C. ligusticus, C. veluchensis

subglobose, flattended

C.pelistericus, C. scardicus, C. cvijicii, C. variegatus Hoppe & Hornsch.



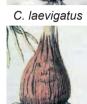
### depressed-globose to ovoid

C. chrysanthus



ovoid

C. boryi, C. tournefortii, C. niveus, C. goulimyi, C. asumaniae, C. baytopiorum, C. suaveolens BERTOLONI, C. almehensis, C. aerius, C. cyprius, C. hartmannianus, C. adanensis, C. leichtlinii, C. caspius, C. antalyensis, C. olivieri, C. vitellinus, C. balansae GAY, C. graveolens, C. hyemalis, C. carpetanus, C. nevadensis, C. fleischeri



ovoid, flattended at base

C. boulosii, C. kerndorffiorum



subglobose, flattended at base

C. moabiticus, C. oreocreticus, C. michelsonii, C. alatavicus, C. korolkowii



depressed-globose

C. banaticus, C. robertianus, C. dalmaticus, C. nudiflorus, C. scharojanii, C. vallicola, C. autranii, C. ochroleucus, C. vernus, C. heuffelianus Herbert, C. tommasinianus, C. longiflorus, C. speciosus, C. pulchellus



depressed ovoid

C. kosaninii



depressed-globose, flattended (disc-like)

C. karduchorum, C. gilanicus



elongated-ovoid

C. versicolor



depressed-globose, flattended at base

C. pallasii, C. thomasii, C. flavus



narrowly ovoid

C. pallasii, C. thomasii, C. flavus



flattened globose

C. etruscus, C. danfordiae, C. biflorus



broadly ovoid

C. serotinus



C. hadriaticus

Fig. 5: Basic shapes of crocus corms: typical example, characteristics of corm shapes, species with equal or very similar corm shapes (drawings from Maw, 1886).

# 2. MORPHOLOGY AND PHENOTYPIC CHARACTERISTICS

### 2.1 Corm-shape and composition

The width of the crocus corm-body is invariably greater than its height. The basic shapes of crocus corms are presented in Fig. 5. We decided to present the different shapes of corms including their tunics as it is harmful for the plant to remove this essential protection only for determination. As can be seen in Fig. 5, most of the crocus corms are ovoid, subglobose and depressed-globose and they can be somewhat flattened or flattened at the base. All other shapes play only minor roles. In some cases it might be difficult to determine the shape exactly as there are transitional forms.

The young corm (1-2 years) is in many species somewhat eccentric, which means the base is obliquely situated in the soil rather than horizontal with a larger development of corm-mass on one side of the growth-axis (Fig. 6). The main content of a mature crocus corm is very nutritious having energy-rich substances accumulated, necessary for the start of the new season after dormancy. This can be seen from analytical data elaborated for C. vernus in its dormancy period in November. The main content is starch (48%), followed by water (39%), sugar (6%), N-containing albuminous compounds (3.2%), cellular fibre (1.4%), mineral matter (1.1%), and oil (0.6%) (MAW, 1886). The surface of the corm is covered with numerous little papillae which seem to be undeveloped buds. According to Maw (1886) ... "some species produce these bud-growth all over the corm and in some species this growth developing as stolons from various parts of the corm, ...or the buds are abundantly developed as bulbils, or cormlets, round the circumference of the old corm. and remain for the first year without producing foliage." Most important of the corm is the production of roots. It is very interesting that there is no relation of root production and the size of the corm. Also, the size of the corm is not related to the size of flowers. Instead, a large production of roots is directly related to the floriferous power of a crocus.

### 2.2 Calcium-oxalate crystals in the corm tunics

Calcium-oxalate crystals in plants are known for some time and comprehensively dealt with in Franceschi (1980). In *Crocus* they were discovered for the first time by Wolter (1990) who found them rather hidden in the corm tunics of almost all taxa known at that time, using special treatment techniques to isolate and observe them under polarized light. He tried also to make a systematic attempt to the genus using this parameter based on and compared to the one of Mathew (1982). As the crystals show not a great variation, what can be seen from Fig. 7, this systematic approach left more questions than answers. However, some results concerning the oxalate-crystals in crocus corm-tunics are remarkable and worth mentioning here. They are shown in the light of the recently established phylogeny of the genus (HARPKE et al. 2013).

The calcium-oxalate crystals are according to WOLTER (1990) "a feeding repellent, which may have played an important role in the evolution of *Crocus* geophytes". The crystals are orientated in all species along the dead vascular-bundles of the corm-tunic

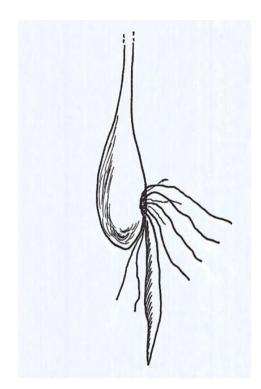
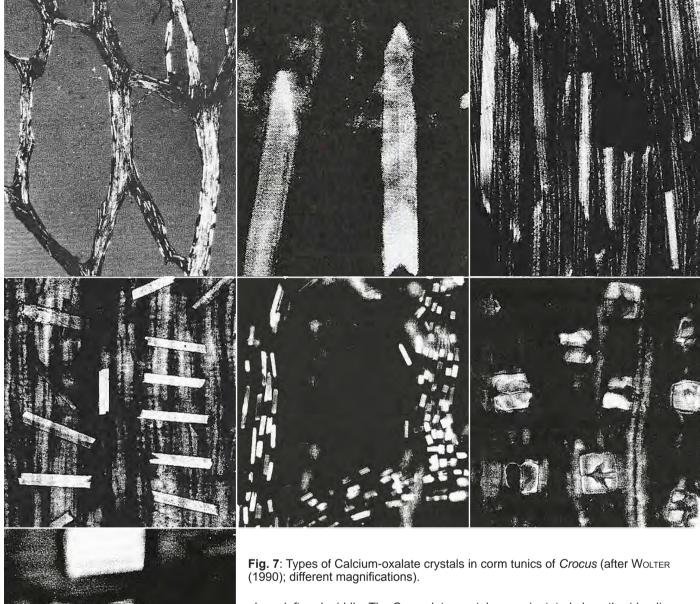


Fig. 6: Eccentric young corm in soil.

**Table 1**: Phylogeny of Crocus according to HARPKE et al. (2013) in correlation to Ca-oxalate crystal-types of species

section Crocus	crystal-type
C. goulimyi	Plarge
series Scardici	N
series Longiflori	N
series Versicolores	N, rarely sand-like
C. ligusticus	N
C. malyi	N
series Verni	N
C. banaticus	N
series Kotschyani	N
series Crocus	N
C. niveus	N, rarely sand-like
Sieberi species complex <sup>1</sup>	N, few sand-like or no crystals
section Nudiscapus	
series Carpetani	N or no crystals
series Orientales	N
series Laevigati	N (or sand)
Adami species complex <sup>1</sup>	at present N + P or no crystals
series Aleppici	N
series Flavi	N
new series with C. gargaricus	N
new s. with C. kernd./leichtl.	N transversal + P
series Reticulati newl. def.	N, sand, P
several newly to define and to	P  or  P + N
establish series with C. cancellatus,	
C. speciosus and former C. biflorus	
subsp.	

<sup>1</sup>series has to be defined in a new systematic of the genus N = needle-like crystals; P = prismatic crystals



above left and middle: The Ca-oxalate crystals are orientated along the (dead) vascular bundel of the tunic of *C. imperati*.

above right: In *C. vitellinus* the crystals are not fixed to the orientation of the vascular bundle.

middle left: Only in *C. leichtlinii* the crystals are orientated transversal to the axis of the vascular bundle.

middle: Needle-like and rectangular crystals together in *C. mazziaricus* Herbert. middle right: The square crystals of *C. chrysanthus* and some other species have a special fine-structure.

below: Biggest prismatic crystals of the genus has C. goulimyi.

except for *C. leichtlinii* in which they are orientated transversal to these. About 90% of the crystals are needle-like with a mean length of 120  $\mu$  and a mean width of 7  $\mu$ . In some cases the crystals are rare in other cases they are very small and sand-like or, in few cases, totally missing like in *C. fleischeri* which might be an effect of the basic soils (pH > 8) in which it mainly

grows. The other crystals are prismatic and have different sizes and surfaces. Finally combinations of these crystal-types occur in some tunics. To get information about their distribution in the genus and of their systematic relevance a comparison of the recent phylogenetic groupings with the crystal-types is presented in Tab. 1.



Fig. 8: Parts of the tunic of different species.

At first the special position of C. goulimyi is clearly visible, being the only one of section Crocus having prismatic crystals which are also the largest ones of the whole genus. Its special position, possibly attached to series *Longiflori* of Mathew (1982), is indicated by this parameter. Secondly the results show, that otherwise prismatic crystals only occur in section Nudiscapus, which of course confirms the actual division of the genus into two sections. Different to these the former subgenus *Crociris* represented by the single species of C. banaticus cannot be confirmed as it has needle-like crystals like those of series Verni to which it is attached in molecular- systematic analyses. The next remarkable findings are the transversal oriented crystals of C. leichtlinii. It has to be investigated yet if this is also the case in C. kerndorffiorum because these two species build a quite distinct genetic group deserving to become a series on its own. Wolter (1990) could hardly distinguish series Reticulati and Biflori of Mathew (1982) regarding their crystal-types. He found 11N and 2P species in series Reticulati and 7N and 4P species in series Biflori of Mathew's systematic. This finding aroused in him the question if the separation of these two series is still justified. As we know now this question is obsolete because series Reticulati is now newly defined (HARPKE et al., 2014) and, concerning the oxalate-crystals, also has a clear structure with only needle-like and sand-like oxalate-crystals, at least for those species, which are comparable and were known to belong to this series at that time. Series Biflori cannot be maintained at all at the present state, as its members occur phylogenetically widely distributed in section *Nudiscapus* and will be assigned to new and reorganised series, which have to be established.

### 2.3 Conditions and shapes of corm tunics

Corm tunics in crocus are homologous to the leaves and significantly more variable from species to species than in other genera of the *Iridaceae*, like, e.g., *Gladiolus*. It was, until detailed phylogenetic alliance among species came to light, one of the more important morphological parameters to divide the genus into groups, used by almost all former authors who made a systematic approach to the genus. Basically there are two parameters of tunics, which have to be considered.

First, there is one or few outside tunics and several to many inside tunics, which are in general of different conditions. The outside structures of the tunic result from the instability of thin and weak tissue materials, which is usually between the (dead) vascular bundles and in some cases are quickly decomposed due to soil acids, bacteria, and fungi. The remainders are the more stable wood-like substances building the backbone of the outer tunic, which is so characteristic for many species. The inner tunics are generally protected from (partly) decay for at least a year until they are pushed outwards by the new one. They are mostly membranous even in fibrous tunics (the caps are in all kind of tunics membranous) (Fig. 8), and usually with less specific markings than the outer ones. Is the decay of the tunic material quick like in wet-soil conditions only one to three tunic-layers can be found around the corm with less significant markings as it would be under more dry conditions. In these cases it is not useful anymore to distinguish between inside and outside tunics. Examples for this are, e.g., C. pelistericus and C. veluchensis.

Secondly, there are fibrous and non-fibrous tunics. The outside of the fibrous ones can have membranous tissue be-

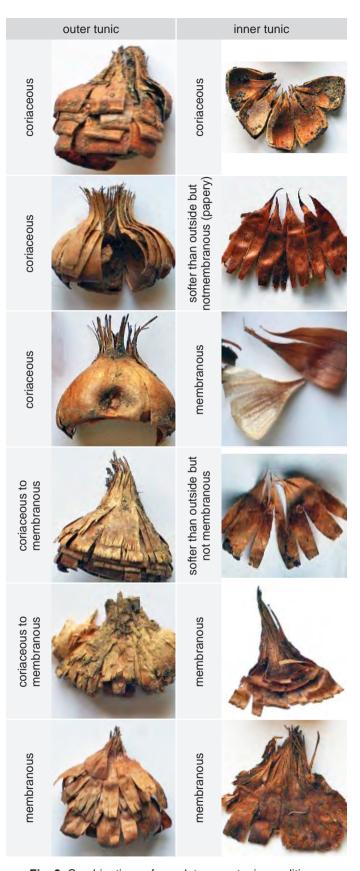


Fig. 9: Combinations of annulate corm tunic conditions.

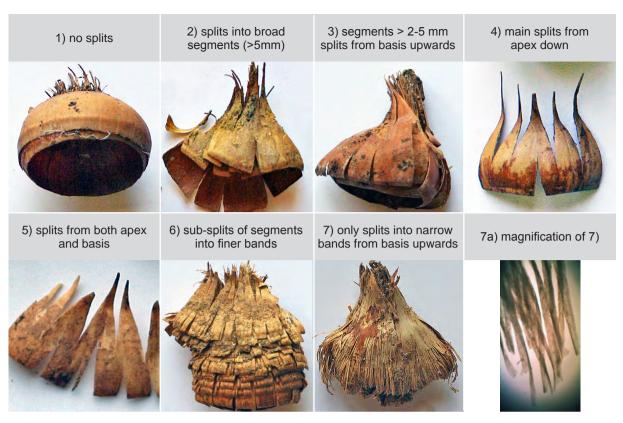


Fig. 10: Types of annulate corm tunic splits.

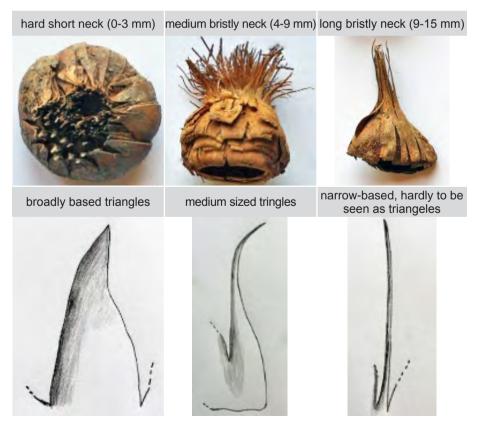


Fig. 11: Examples for neck formation of annulate species.

tween them or not. The fibres can be interwoven, parallel or reticulate or a combination of the latter two. The fibres can have different shapes of cross-sections and different diameters (Fig. 13). In reticulate tunics also the interspaces can be different. Non-fibrous ones have either a more or less entire tissue (outside and inside), which can be coriaceous or membranous and split into broad or narrow segments, or band-like stripes of different length, diameter, and cross-sections, with rings at base (annulate tunics) or without.

### 2.3.1 Non-fibrous annulate tunics

Annulate corm tunics belong to the non-fibrous ones and are characterized by having a more or less entire main tunic, which can split in very special ways and frequently form rings at the base of the tunic. In the genus *Crocus* many species exist which have these rings at the base. Remarkable is that all of these are confined to section *Nudiscapus*. In the recent phylogeny they can be found in several but different series (parallel evolution of this character). As this will be a matter of a greater change in the future systematic of the genus, names of series, which have to be reorganized or newly created as well as species names are not mentioned here. Instead, a systematic approach to annulate corm tunics is presented for the first time which was worked out of approximately 200 different samples of at least 60 different known "annulate taxa". It is the basis of a special tunic-key of annulate species, which is presently in preparation.

As a result of the investigation four parameters turned out to be important, as they have sufficient differences to be dealt with in detail: 1) corm tunic material, 2) corm tunic splits, 3) neck formation, and 4) ring characteristics

### Corm tunic material

The annulate corm tunic consists of wood-like material mainly containing cellulose. Therefore, most corm tunics show low decay-rates in soils and are persistent for many years, at least in semi-arid locations. Main types of annulate corm tunic material are systematically arranged in Fig. 9. This scheme is rather precise compared to the simple view, which was used until today but it is still relatively coarse compared to the real conditions in nature, which show even more subtle transitions between all groups. Despite this it covers all existent material-types of annulate crocus tunics and is sufficient to distinguish between major groups of tunic material. Coriaceous tunics (hard, eggshelllike) are the most common ones. Transitional forms, which are softer but not really membranous (papery), are not as frequent. The membranous ones are clearly different to those but also less frequent compared to the coriaceous ones. In most cases they are very thin and papery, the inner ones sometimes transparent and very susceptible and fall easily apart when dry.

### **Corm tunic splits**

In the past no attention was paid to tunic splits but they deserve to be looked at closer as they are rather diverse and can be helpful in species separation. A systematic approach to observable splits of annulate corm tunics is presented in Fig. 10. The example in Fig. 10-1 is rather rare. Special conditions seem to be necessary not to split the tunic, like insufficient growth of

the new corm. The cases of Figs. 10-2 to 10-3 are numerous. Interesting is that splits from the neck downwards and from the basis upwards never meet which is obviously necessary not to destabilize the tunic (Figs. 10-4 and 10-5). Tunics with sub-splits and/or notches (Fig. 10-6) are less frequent and the ones which split only into fine bands are rare and until now only observed in C. aerius and C. fibroannulatus. Interesting is the absence of rings with C. aerius and their presence with C. fibroannulatus. This also means that these two species do not have fibrous tunics as previously assumed but finely banded ones. This is clearly visible under the microscope (Fig. 10-7a). These findings correlate perfectly with the results of phylogenetic ITS –analyses, which show no separate positions for these two species. Instead, C. aerius (Figs. 10-7 and 10-7a) and C. fibroannulatus are positioned among their relatives, which do not have these splits into fine bands. Unfortunately, we were not aware of this fact when naming C. fibroannulatus, which would have been named better "C. fasciarius-annulatus" (Fig. 10-7a).

### **Neck formation**

The neck of annulate corm tunics is generated by more or less deep down-splits from the apex of the main tunic. The length can be different and number of splits as well as distances between the ends of the splits creating differently shaped and sized segments. If one connects the ends of the splits one can imagine "triangles" as a result with different lengths of bases as shown in the drawings of Fig. 11. Between the extreme examples of Fig. 11 (left side) (broadly-based triangles form hard and short necks) and Fig. 11(right side) (very short based triangles, hardly recognizable as such, form very long and bristly necks) all kinds of transitional forms were observed. A medium sized bristly neck is represented in Fig. 11 (middle).

### Ring characteristics

Rings at the base of annulate tunics are an important taxonomical parameter, which morphologically reflects the genetic division of the genus, as these can only be found in section *Nudiscapus*. But this feature is rather more complex as previously thought and shows many well-marked characteristics, which are suitable for morphology-based species identification. A systematic approach to this interesting parameter is shown in Fig. 12. Coriaceous rings are the most frequent ones and those without teeth are more abundant than those with teeth. Of those having teeth the ones with many but short teeth are more abundant than those with long teeth. Annulate crocuses having membranous rings (they also must have a membranous corm tunic) are not so frequent and obviously none of those have teeth.

Likewise to the corm tunic material, the splits, and the neck formation there are very fine-patterned transitions of ring-characteristics in the investigated more than 150 different tunics, which cannot be transformed into a manageable system. However, the presented systematic approach to evaluate four of the most important parameters of annulate corm tunics in the genus *Crocus* is by far the most comprehensive one developed until now. It will significantly help to differentiate and to identify the increasing number of annulate crocus species. A systematic characterization of non-annualate and non-fibrous tunics is also in preparation.



Fig. 12: Ring characteristics.

### 2.3.2 Fibrous tunics

The outer fibrous tunics are characterised by thin (smooth) to thick (hard) fibres with all kind of transitions and different cross-sections. In most cases circular/near circular (irregular) or band-like cross-sections of fibres occur, in few cases they are misshapen quadratic to rectangular (Fig. 13). The narrow elliptically ones are oriented longitudinally and vertically away from the centre of the corm giving the impression the fibres consisting of bands (Fig. 13). The fibres are either parallel, reticulate or a combination of both or interwoven, and can have membranous tissue in between or not. The reticulation can be narrow or wide and have short or long interspaces. In rare cases the narrowly reticulate fibres at the apex widen into narrow unorganised bands towards the apex (C. serotinus) or vice versa, which means the fibres get thinner from the apex towards the base accompanied by diminished interspaces of the reticulation (C. sieberi). The inner tunics of fibrous tunics are in general membranous and only in few cases also fibrous like, e.g., in C. carpetanus (Fig. 14).

Crocus sieheanus has to be mentioned here as it has a special tunic which was not really understood well until today. The coriaceous tunic has two different kinds of splits. One, consistent of small parallel bands of about 0.5 mm width is from the base upwards to the centre of the tunic. The other one, which splits shortly down from the apex, is tooth-like and creates a crownlike neck. Both types of splits never meet. The corm accumulates tunics of previous seasons on top of each other, which results in a very distinct shape (Fig. 14). One feature we found as part of this tunic was never recognised before: occasionally occurring rings at base (Fig. 14). These are also very peculiar having many teeth (almost side aside) and are connected by a thin membranous tissue (Fig. 14). Even on these characters alone it is clear that C. sieheanus cannot belong to series Reticulati, which was proofed in a recent publication of us by phylogenetic analyses (HARPKE et al., 2014). Therefore, its future place will be in a new series together with species like C. danfordiae, C. minutus, C. caelestis, C. leucostylosus, C. weldenii, and C. stridii.

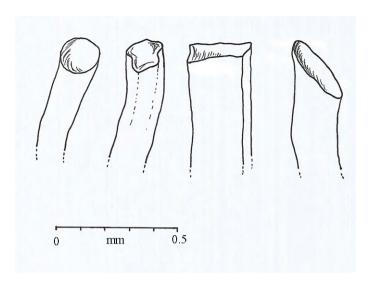


Fig. 13: Cross-sections of fibres and bands.

### 2.3.3 Determination key for Crocus species or series based primarily on the structure of the corm tunic

This determination key is the first one of its kind for *Crocus*. Although the present version cannot include all species due to necessary major changes in the systematic of the genus, especially of section *Nudiscapus*. However, it shows that it is possible to identify species and series predominantly using characteristics of the corm tunic. An extended version of this key will be presented in the revision of the genus.

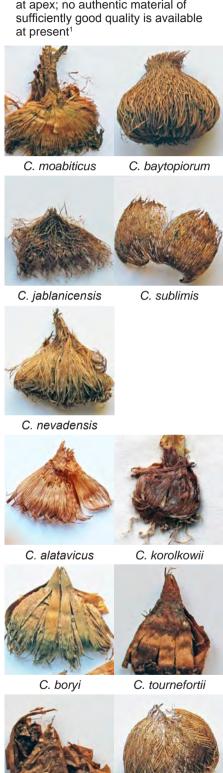
Using this key one should have in mind that a proper identification of species and series is dependent on authentic material from original localities. If there is the need to use tunics from pot-cultivated specimens or from open ground one has to grow the crocuses at least three years undisturbed in pots (or ground) before harvesting the tunic during dormancy. The main reason for this is that growers mostly "clean" the corm when re-potting it every year which actually means they remove the old tunics. So, in the best case, only two layers of tunics are present, the new one and the one of the previous season, which, as a rule, does not have all the necessary characteristics for determination.

1	outer tunic fibrous	3
1*	outer tunic non-fibrous	2
2	tunic entire or with different splits having rings at base a special key for annulate tunics is presently in preparation	on
2*	tunic not annulate	4

3 3*	inner tunic also fibrous
4 4*	tunic coriaceous or slightly softer; splits into narrow bands or broad segments or teeth of different shape or arrangement $\dots$ 6 tunic softer to membranous mainly splits into fine ( $<$ 0.5 mm) or broader (around 2 mm) parallel vertical bands $\dots$ 7
5 5*	tunic of parallel fibres
6	tunic splits broadly into triangular teeth from the middle of the tunic slightly curved inwards at base, tunics of previous seasons never organized like roof tiles
6* 6**	tunic splits broadly into triangular teeth strongly curved inwards at base, tunics of previous seasons always organized like roof tiles
7 7*	tunic splits into bands of 2 mm width or more with or without sub-splits at base
8 8*	tunic splits without sub-splits
9 9*	tunic membranous splits into bands of about 1 mm from base only to 1/3 of the tunic
10 10*	splits band-like, bands less than $< 0.5$ mm broad and up to half of the tunic
11 11*	fibres fine and finely interwoven
12 12*	fibres fine and finely reticulate, becoming thicker towards apex and interspaces of reticulation smaller towards base
13 13*	tunic wholly reticulate
14 14* 14**	fibres fine and still connected by thin membranous tissue 19 fibres fine without connection of membranous tissue 20 fibres coarse and coarsely reticulate $a \rightarrow \text{flowers yellow}$
15 15*	fibres fine to coarse and coarsely reticulate species of series <i>Reticulati &amp; C. baytopiorum</i> (series <i>Crocus</i> ) fibres fine and finely reticulate
	fibres parallel throughout or occasionally anastomosing at the apex
17 17*	fibres very fine (ca. 0.2 mm in diameter) → species of series <i>Versicolores</i> (including <i>C. malyi</i> ) and species of series <i>Orientales</i> fibres parallel only in the lower part, upper part membranous
18 18*	fibres broadened and flattened from apex towards base with interspaces becoming wider and ending as unarranged bands (Fig. 14)
19 19*	fibres parallel at base and weakly reticulate at apex
20	fibres coarsely reticulate
20*	fibres finely reticulate corm only 5-8 mm in diameter

Section Crocus

C. kotschyanus and the other members of this series have thinly membranous to fibrous tunics, the fibers are parallel at base, finely reticulate at apex; no authentic material of sufficiently good quality is available at present<sup>1</sup>



C. veneris

C. fleischeri

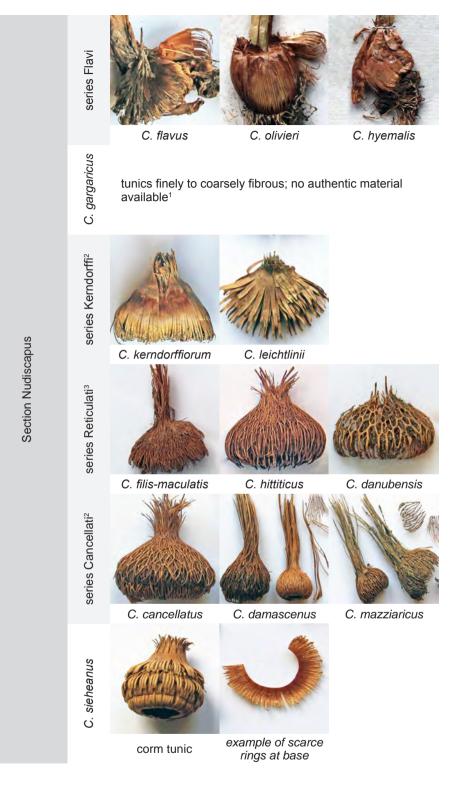


Fig. 14: Examples of fibrous and non-fibrous corm-tunics (annulate species excluded) according to phylogenetic groups of the genus (HARPKE et al. 2013)

<sup>1</sup>In the revision of the genus authentic material will be presented.

<sup>2</sup>A new series which has to be established in a new systematic of the genus.

<sup>3</sup>This series was reorganized by HARPKE et al. (2014).

### 2.4. Sheathing leaves (cataphylls)

Cataphylls are developed around the corm at the base of the crocus and protect the ascending flower-buds. They are much broader than the true leaves. In general three to six cataphylls occur, ordered in decreasing length from inside to outside. Their expanded bases annually form the main corm tunic. The inner one is spathulate above and tubular below. The outer one is mainly a tubular membrane with differently shaped edges on top. There is some variability in shape, condition and colours as can be seen from Fig. 15. In most cases the membranes of the cataphylls have more or less pronounced veins without distinct colouring. Examples for this are C. ochroleucus, C. hyemalis, and C. adanensis (Fig. 15). Crocus korolkowii and C. dalmaticus have whitish cataphylls, the first one with brown tips, the last one with greenish tips. With C. hermoneus the membranes have a brownish tinge all over and C. asumaniae has pronounced brownish-vellow edges of the cataphylls. Other species have brown-speckled cataphylls like C. goulimyi. Crocus corsicus gets a brown membrane with brown veins and with C. roseoviolaceus the outer cataphylls are aged to a complete brown in contrast to the inner ones which are still white (Fig. 15). The young cataphylls of C. marasensis are white, become brown with age and persist at least to the next season (Fig. 15). The young cataphylls of *C. flavus* have a brownish tinge and brown veins before they become totally brown with age (C. flavus 2) and persist for several seasons. With a not vet determined species of the Adami complex the cataphylls are completely yellow (Fig. 15). In other species like C. fibroannulatus, C. fleischeri, and C. leichtlinii the membranes are of a light green with greenish or greenish-vellow veins. Green membranes and deep green veins occur in C. kosaninii and especially C. pestalozzae. Very remarkable cataphylls has a crocus of which Brian Mathew was not sure to accept it as a distinct taxon, C. lazicus, described by Boissier (1866, 1866a). Besides the almost sessile ovary at flowering-time and a leafcross-section very different to the one of C. scharojanii, treated by Mathew (1982) as a synonym, the cataphylls of C. lazicus are the shortest of all Crocus species, called by Maw as almost abortive. Even the prophyll overtops them largely and is visible, a unique feature in the genus (Fig. 15 lower right). Maw (1886) regarded it as species without any near ally and we also think that it is a distinct taxon well worth looking for although this could be a rather exhaustive task considering the story about its discovery.

### 2.5 Prophyll, bract, and bracteole

The foliaceous appendages to the ascending axis are prophyll, bract, and bracteole. They have two different origins. The prophyll is, if present, developed from the base of the pedicel and has an addorsed position to the main axis (Fig. 33). It is a membranous tube enclosing the pedicel and mostly reaching the ovary. Bract and bracteole are growing from the base of the ovary (Fig. 33). In *Crocus* the bract is tubular and always present on the contrary to the bracteole, which is ligulate and can be present or absent. Up to now these three types of foliar organs play an important role in dividing the genus into systematic entities. In the last systematic approach by MATHEW (1982) the subgenus *Crocus* was divided into two sections, one with species having a prophyll (*Crocus*) and one with species lacking a prophyll (*Nu*-

discapus). Unfortunately, now this simple division cannot be maintained in the present state any longer as phylogenetic analyses brought up some results, which force us to alter this systematic concept to some extent. The reason for this is predominantly C. sieberi and its allies, at present C. sublimis, C. atticus, C. nivalis, C. dalmaticus, C. cvijicii, C. veluchensis, C. robertianus, C. rujanensis, C. jablanicensis and at least one more new species yet to be described. They all lack a prophyll and have fibrous reticulate corm tunics. Due to this they are placed presently in section Nudiscapus but genetically they clearly belong to section Crocus (HARPKE et al., 2013). It will take some effort to clarify and revise this situation yet.

Despite the systematic importance these leaves also show variation in length and width as well as in colours (Fig. 16). Sometimes they reach the middle of the flower and can be rather conspicuous. Most of them are silvery-white very thin and membranous. Crocus asumaniae and C. cancellatus sensu lato (Fig. 16) are examples for rather inconspicuous bracts and bracteoles. which slightly overtop the cataphylls and are closely attached to the perianth tube or spread starry outside (C. cancellatus 2 of Fig. 16). Bract and bracteole of C. candidus are both long attenuate and almost of the same form and size. With C. cyprius the bract is much broader than the bracteole and flattened at top. Crocus abantensis has conspicuous silvery bracts and bracteoles, both broad and peaky at top. Bracts and bracteoles of C. alexandri have a brown tinge and the ones of C. corsicus are rather tubular. Very interesting are the soft lilac ones with violet veins of C. ancyrensis from near Gerede, province Ankara (L+P 7081). Remarkable are those of C. boryi, which have intense green veins more or less strongly reticulate. The same can be said for the bracts of C. nudiflorus and C. vallicola. Also remarkable are bract and bracteole of a C. chrysanthus population from Ulu Dağ, province Bursa (P 8044), Turkey, which have deep violet mainly vertical veins slightly disorganised at top. Last but not least the conspicuous bracts and bracteoles of *C. artvinensis* are very broad and skinny having brown tips on top and the ones of C. flavus are totally light brown.

The prophyll is, except for *C. lazicus*, only visible when the flower is dissected. To protect species and genus a dissection for determination purposes cannot be recommended by us, as there are many other possibilities to identify a crocus.

### 2.6 True leaves

The upper cap-like corm tunics are just the expanded bases of the cataphylls and the true leaves. This is the reason why the leaf-structure correlates with the structure of the corm tunic, which means there are theoretically as many varieties of corm tunics as there are of leaves. This sounds surprising but can be seen when looking closer at the leaves of different crocus species, which show a large variety concerning almost every parameter. The true leaves are attached to the caps of the tunic and are invariably much longer than broad. These vary in form, colour, white stripe, ribs in the grooves of the backside of the leaf, hair, diameter, length, and peculiarities of cross-sections. Like with all the other parts of the crocus there are uncountable transitional forms, which often make it difficult to define a colour, form, or other parameter in a specimen to be investigated. Some works have been made on this topic in the past of which

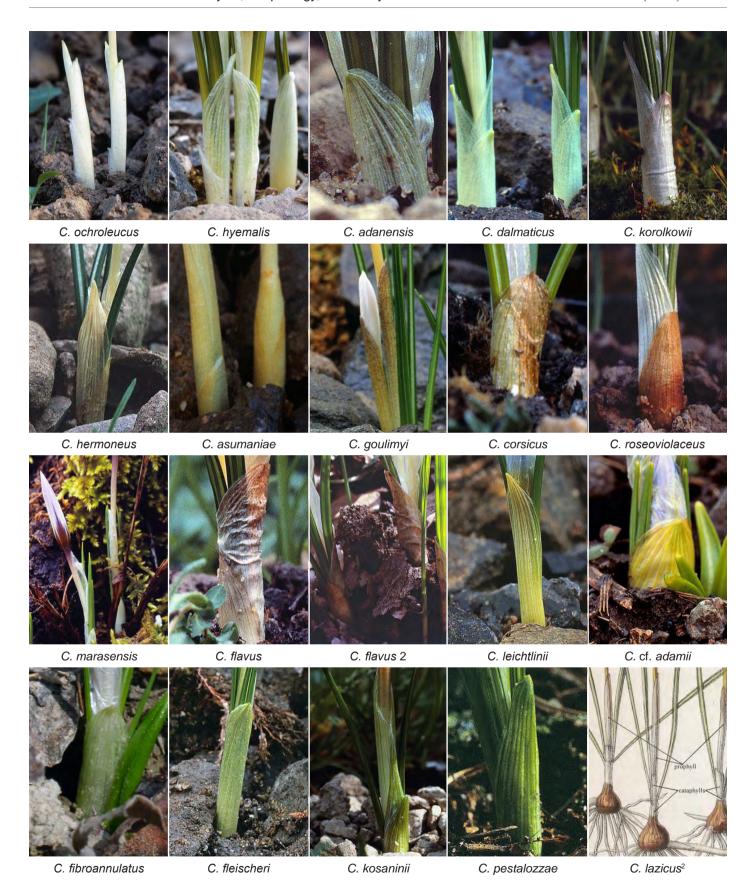
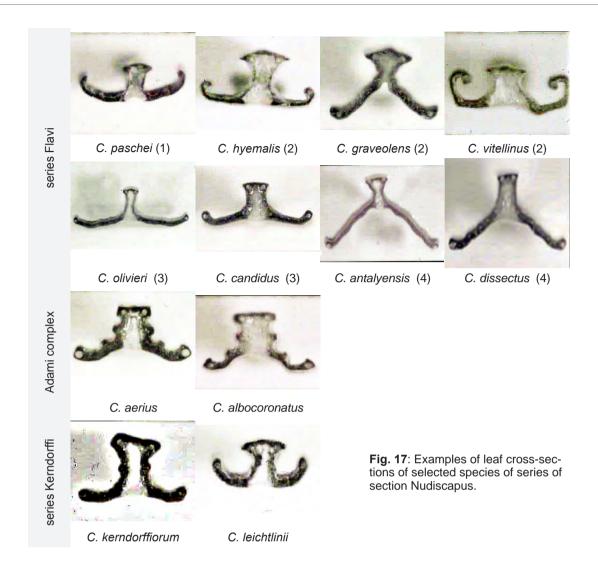


Fig. 15: Variability of cataphylls¹ (¹details from photographs of Erich Pasche; ²extract from Maw (1886)).



Fig. 16: Variability of bracts and bracteoles.



the one of RUDALL (1990) is the most detailed one with 52 taxa investigated. However, almost a quarter of a century later around 200 or even more species of *Crocus* are known and are awaiting to be investigated systematically including parameters of their true leaves. One of these parameters turned out to be highly relevant for taxonomy, the shape of the transversal cross-section of the leaf at its widest part as it was already assumed by RUDALL (1990). In Fig. 17 examples of leaf cross-sections are presented for species of section Nudiscapus. The differences between species and between series are immediately visible. According to the recent phylogenetic tree of HARPKE et al. (2013) series Flavi is represented by four separate branches. A first one by C. adanensis and C. paschei, a second one by C. graveolens, C. hyemalis, and C. vitellinus, a third one by C. olivieri and C. candidus and a fourth one by C. antalyensis and C. dissectus (Fig. 17). Also the compared species of the newly to be established Adami and Kerndorffi complexes show highly similar structures but

very different ones to series *Flavi*. It can be seen that the results of the phylogeny and of the leaf cross-sections are very well correlated. Therefore, for the revision of the genus we plan to investigate more, especially the new taxa of the genus.

### 2.7 The perianth

The perianth (flower) of a crocus is in most cases rather spectacular although of a simple beauty. It is admired by many when coming up as a sign of spring or by enthusiasts who often contest their photographs of crocus flowers of different species. To understand how beautiful crocuses really are one has to visit them at their natural growing localities and see them embedded in their plant communities, which can be of course very diverse but, together with the crocuses, always represent a harmonious picture.

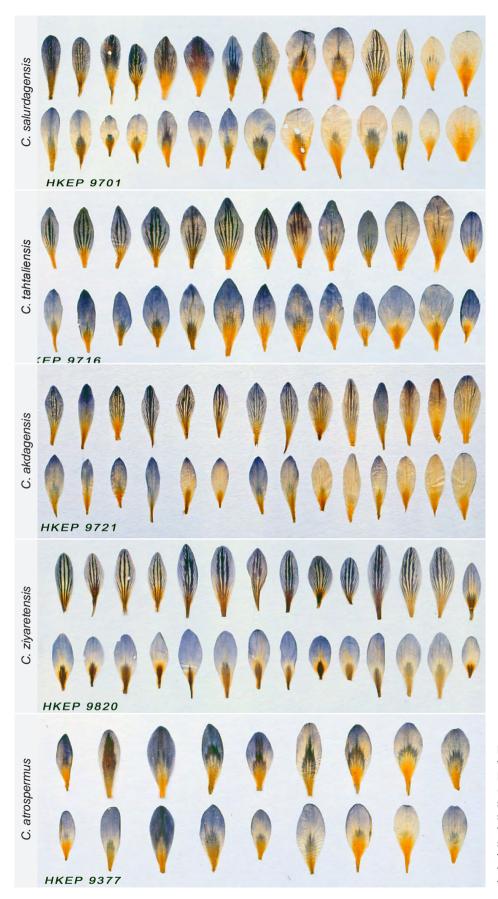


Fig. 18: Examples of segment variations of five taxa of section Nudiscapus of five localities. (Upper rows represent outer segments, lower rows inner segments; both rows show the outside of segments. The segments were prepaired of frehly collected flowers and then immediately photographed to maintain original colours).

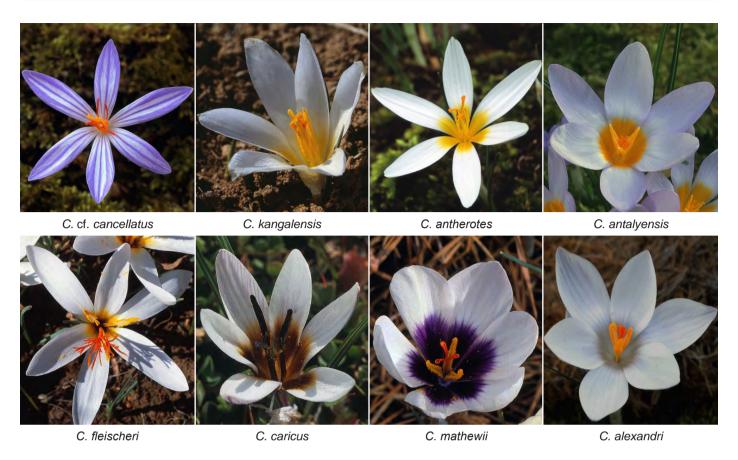


Fig. 19: Examples of throat colours.

### 2.7.1 Segments

Crocus has segments orientated in two whorls of three segments each. The outer segments are in general a bit longer than the inner ones but the inner ones are on average broader than the outer ones. The segments consist of three layers of cells, which can be coloured differently. This has the effect that inside and outside colouring as well as inside and outside markings are often very different with the tendency to spectacular outsides of the outer segments and rather inconspicuous ones of the inside ones. Especially the outside of the outer segments is often marked intensely with stripes or featherings, the inside ones are on both sides much less conspicuous more uniform with less and faint speckles, stripes or spots. In general the segments of crocus species are greatly variable considering their sizes, shapes, colours, and markings. Indeed, they vary so much in all these characters not only from one species to another but also within populations from individual to individual of the same species that one hardly can find characteristics which are really stable. To illustrate this complex situation we compared between 18 and 30 single segments of five different taxa of five different populations of species of section Nudiscapus (Fig. 18). From this it is clear, that almost all kinds of segment sizes, segment shapes, segment colours and markings can occur even in one population of one species but with a large overlap to other species. This most considerable overlap of these parameters between species

binds a determination of *Crocus* species in many cases to statistical evaluations rather than to individual ones (chapter 3).

### 2.7.2 Tube and throat

The perianth tube outside cell layer has not so much variation as one can assume. It is invariably tube-like with partly irregular cross-sections. In some species it is very long (C. goulimyi) or very short (C. cvijicii) and in the lower parts mostly white (colourless). Towards the segments it can get striped or speckled frequently violet or violet-blue or the whole tube is coloured brownish-violet or built a transition to dark violet-brown or otherwise coloured spots in the lower part of the segment. Very different to this are the throats of crocuses inside cell layer, which play an important role as attractors for pollinators. They can be glabrous or hairy, can be reduced to a tiny coloured area or prolonged up the half of the segments. Sometimes there is a different colour deeper in the throat (C. ionopharynx) or as a corona above the throat like in the variation 'Tricolor' of C. sublimis. Besides species with colourless ones and those of which a throat is not really marked as a distinct zone in the flower (C. cf. cancellatus in Fig. 19) there are many yellow species which have the same throat-colour like their segments. Other throat colours can be grey or have different shades of yellow, orange, brownish to deep brown-violet, and intense violet (Fig. 19). In some species like C. vallicola there are only small yellow spots at the base of the throat.

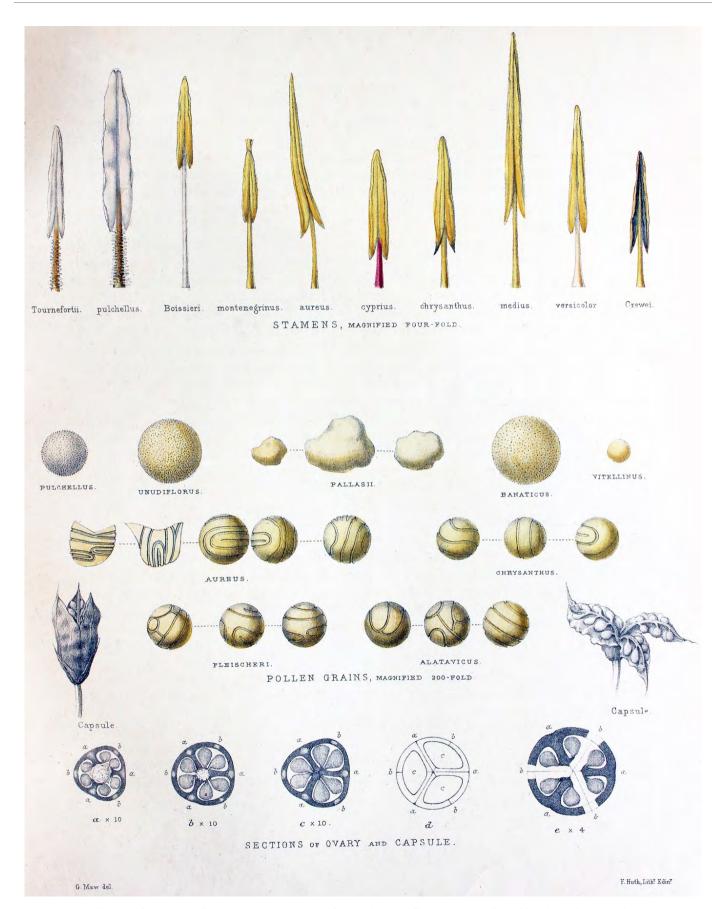
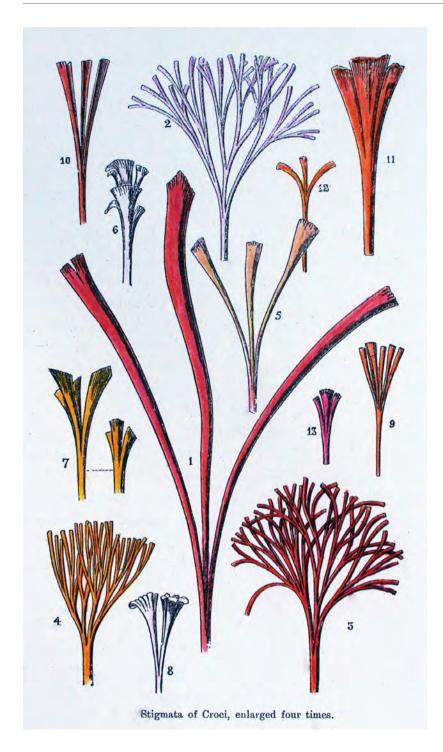


Fig. 20: Stamen, pollen and cross-sections of capsules in different stages (from Maw (1886), altered).



**Fig. 21**: Variability of styles (from Maw (1886), altered).

C. sativus

3

- 2 C. iridiflorus (= C. banaticus)
  - C. medius (= C. ligusticus)
- 4 C. laevigatus
- 5 C. montenegrinus (= C. albiflorus?)
- 6 C. nevadensis
- 7 C. aureus (= flavus)
- 8 C. carpetanus 9 C. olivieri
- 10 C. biflorus
- 11 C. vernus
- 10 C. Verrius
- 12 C. caspius
- 13 C. parviflorus (= C. danfordiae)

### 2.7.3 Filaments

The filaments are predominantly white, light yellow or yellow. In some cases they are deep orange or scarlet like in *C. cyprius* or deep lilac (Fig. 20). Several species have only thinly distributed papillae on the filaments, but in others like with *C. pulchellus* and *C. tournefortii* they are densely papillose. This feature should not be mistaken with the papillae in the throat! Filaments can be rather broad and stiff near base and thin and filiform especially at the connection to the anthers.

### 2.7.4 Anthers, theca, connectives, and pollen

The anthers of crocuses are invariably arrow-shaped (Fig. 20) but vary to a great extent concerning the development of the lobes and the shape of the apex. The lobes can be very short indistinct and just rounded, tightly pressed to the filaments or very long and conspicuous far away from the filaments. The apex can be obtuse or rounded or, rather often, emarginated. The theca is in general the most colourful part of the anthers (Fig. 20). In case the pollen is released the original colour of the anther can be

hidden behind a thick layer of pollen. This can lead to misidentifications especially of black anthers and otherwise coloured connectives. The connectives bind the theca and built the anther. They can be thin and colourless but also broad and conspicuous and of different colours even in one population. Their colours can be identical to the anthers or different. The pollen is either yellow (most of the genus) or creamy to white, as, e.g., in species in series *Kotschyani*, *Laevigati* and *Speciosi*. Although of very different sizes the shape of the pollen is predominantly spherical and the surface is in half of the genus only papillose without any markings. The other half is glabrous, inaperturate or weakly to strongly spiraperturate (Fig. 20). To discover a possible taxonomic relevance a systematic investigation of pollen for the entire genus is necessary.

### **2.7.5 Styles**

The styles in *Crocus* exhibit abundance of forms and colours which can be perfectly seen in Fig. 21. So it is not surprising that one of the former authors dealing with the genus tried to establish a system of *Crocus* based mainly on this character (BAKER, 1873). Unfortunately, this system has a major disadvantage, it connects species together which otherwise have no sign of being relatives. Despite this some distinctive styles are for many species characteristic and useful for an immediate identification (C. banaticus, C. karduchorum). In less clear cases like in all trifid species with only minor variations it is necessary to look closer at other characteristics of the styles as there are a) different shades of colours b) different hierarchy levels of style-divisions which can be in two-fold or three-fold. Furthermore, the length of style-branches can be significant as can be the papillae on the styles. They can have none, few or many which then make them papillose.

### 2.8 Ovary and capsules

The trilocular ovary is perfectly shown by drawings of lateral cross-sections in five developing stages up to maturity and dehiscence (Fig. 20). Morphological differences in seed capsules of crocuses are obviously not so interesting to most of the authors dealing with the genus and are also mostly neglected in new plant descriptions. One reason might be that in case a new crocus is found, the plant is mostly in the flowering state and the seed capsules are in the ground and even if the plant was pollinated, at flowering time they are only poorly developed and not present above ground. Nevertheless, there are different seed capsules in the genus. To find out if they are distinct enough to be of taxonomical value we made a compilation of them. In Fig. 22 seed capsules of species and series belonging to section Crocus are shown in order of the recent phylogeny of the genus (HARPKE et al. 2013). At a first glimpse there seem to be at least only minor differences at least between single species. However, more important are the differences between the series. Crocus goulimyi has a capsule which is not so much different from others as one can assume. It is ovoid with rather obtuse ends (the prolongations in the photograph of Fig. 22 stem from the bract/bracteole) in contrary to species of series Longiflori which have a significantly acuminate top of the capsule. No acumination can be observed in species

of series *Versicolores* which have obtuse tops of the capsules. Elongate ovoid and extremely acuminate are the capsules of *C. ligusticus* which stand in contrast to the obtuse ones of *C. niveus*. The capsules of *C. sieberi* and its relatives are rather small and subglobose to ovoid and distinctly but only shortly acuminate. *Crocus banaticus* has an elongate ovoid capsule which is extremely acuminate like with *C. ligusticus*. Species of series *Kotschyani* have elongate ovoid capsules which are only slightly acuminate. Very distinct and different capsules have species of series *Crocus* which are elongate ellipsoid and rounded on top. Of less interest are the colours of the capsules as a differentiation is hardly possible due to very little nuances of all kinds of brownish.

### 2.9 Seeds

Seeds are normally not present in flowering crocus populations. If one is lucky sporadically a capsule with some seeds of the last season can be found in a population. The best way to get authentic seeds is a later return to the locality when capsules are ripe and pushed above ground to release the seeds. Unfortunately, this is not possible in most cases. An alternative way is an artificial seed production which means one has to cultivate and pollinate flowering specimens. Although cross-pollination is generally rare in the genus it might occur when growing several species aside belonging to the same series. Special attention has to be paid when it is necessary to receive authentic material for scientific purposes especially genetic analyses.

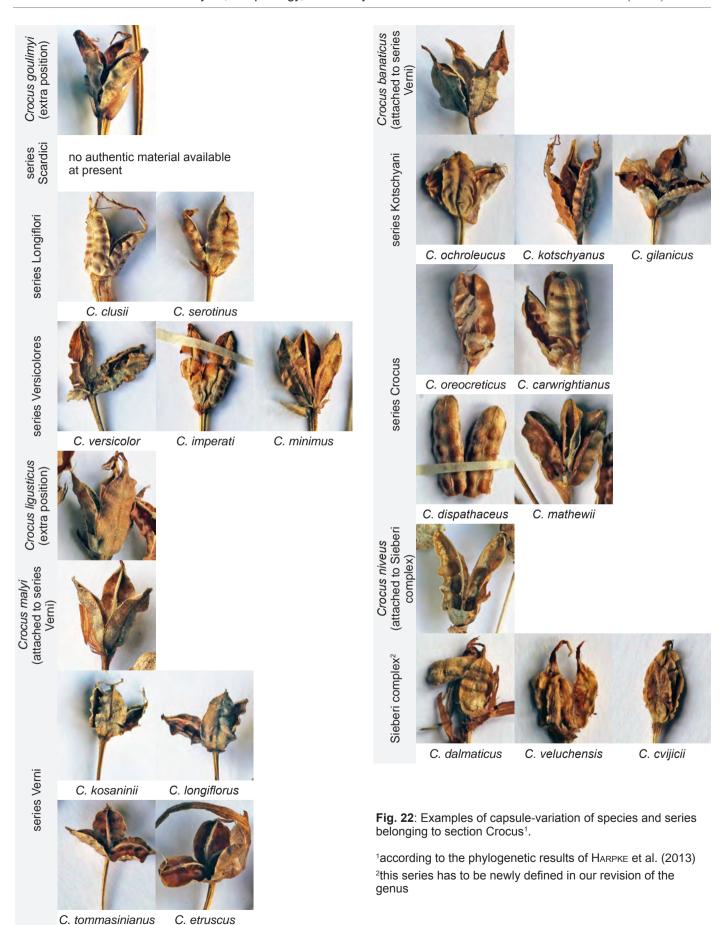
### 2.9.1 Macro-structures of seeds

There are four macroscopic parameters of seeds which can be recognised. It is the form, colour, raphe, and caruncle. The raphe is a longitudinal ridge on the outer seed coat, the caruncle a horny outgrowth near the hilum of the seed that is formed from the integuments. All four parameters can vary to some extent. For comparative purposes the seeds of species of section *Crocus* are presented according to the recent phylogeny of HARPKE et al., 2013 (Fig. 23). The shape of the seeds can be very different as this can be seen from C. pelistericus (narrowly elongated) or C. asumaniae which is almost globose. Looking at the caruncles and the raphes the same can be found although all species in series Versicolores have large and distinct caruncles. From these observations it is clear that an important parameter in this presentation is missing, the colour of seeds. With the colour it would be e.g. possible to clearly separate all species of the Sieberi compex which have a distinct membranous caruncle of a golden-vellow colour.

This means to us that in the revision of the genus only colour-photographs of seeds will be provided.

### 2.9.2 Micro-structures of the seed surface (testa)

Another, most interesting and taxonomically highly valuable aspect of crocus seeds is the microstructure of the testa. This parameter alone is sufficient for a systematic grouping of the entire genus. As this is a matter of a work on its own only a brief example of testa-variations of species of section *Crocus* is



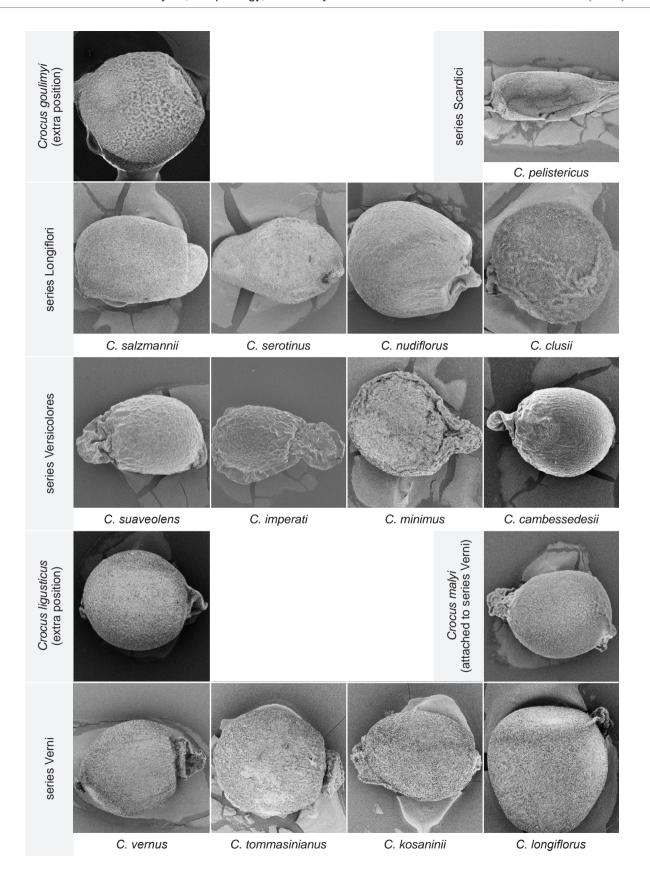


Fig. 23: Variability of seeds by SEM-photographs of species belonging to section Crocus<sup>1</sup>.

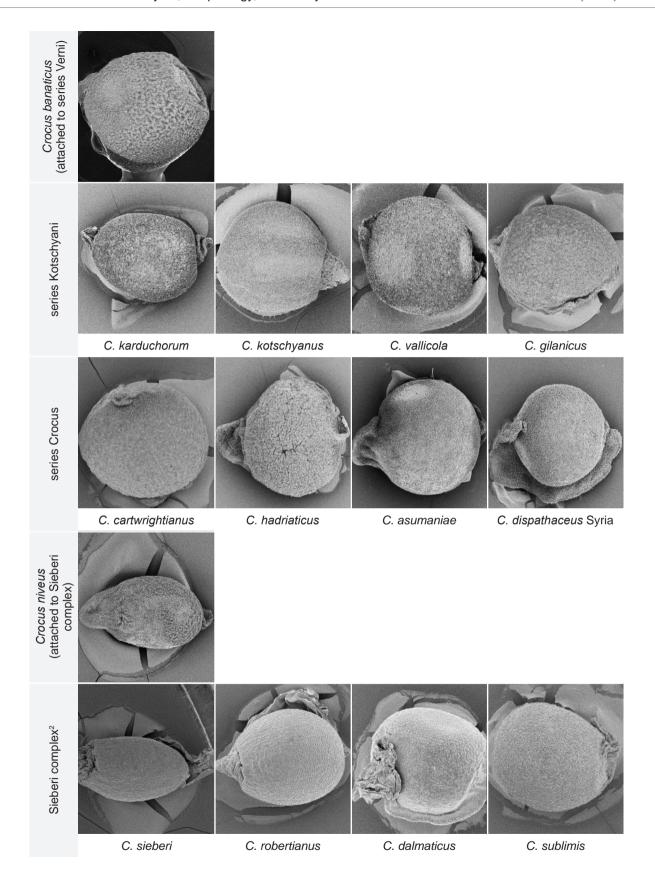
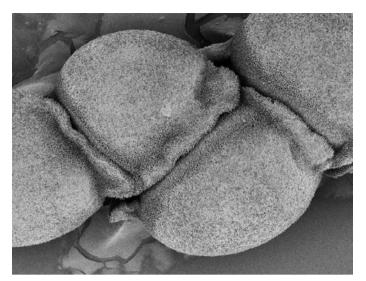


Fig. 23: continued.

<sup>&</sup>lt;sup>1</sup>according to the phylogenetic results of HARPKE et al. 2013. <sup>2</sup>this series has to be newly defined in a revision of the genus.



**Fig. 23**: continued. Attached seeds in the seed capsule of *C. asumaniae*.

shown here to give an impression. The arrangement of the series and of single species occupying extra positions is adequate to the recent phylogenetic results of HARPKE et al. (2013) (Fig. 24). The presented SEM-photographs have to a minor extent a different magnification factor but this has no influence on the possibility to compare the microstructures of the presented testas. The differences of species belonging to different series of section *Crocus* are clearly visible (Fig. 24).

Crocus goulimvi has genetically an outstanding position but a testa comparable to Crocus longiflorus. According to MATHEW (1982) it is connected to series Longiflori. Unfortunately Crocus longiflorus the type species of this series belongs clearly to series Verni (HARPKE 2013 and 2014). Series Scardici occupies a quite distinct position in the phylogeny visible also by the testa example of C. pelistericus although this one has a similarity to the one of C. cvijicii. The two different cluster-twigs creating series Longiflori and Versicolores are perfectly confirmed by the different testas of the species belonging to them. Also confirmed by the testa are the two more or less separate positions of C. ligusticus and C. malyi. Attached to series Verni, the position of C. banaticus in series Verni (formerly thought to be in a subgenus of its own) is also astonishingly confirmed by the testa. Quite distinct are the testas of series Kotschyani and well separable from the testas of species of the connected series Crocus in which C. baytopiorum might have a transitional position which is indicated by its testa having parts of series Kotschyani as well as of series Crocus. Crocus niveus, despite being distantly connected to Sieberi complex a series which has to be newly established, can be easily separated by its testa from members of this new series. All have different but similar testas with common features like the clear separation into segments with or without naps in the centre. All in all this comparison shows the congruence of the phylogenetic clusters with the testa of series and species.

Despite the fact that this morphological parameter cannot be used for the identification of crocuses in the field it has a great taxonomical value. Detailed results as well as a systematic approach to the whole genus using this very interesting parameter is in preparation and will be published elsewhere.

## 3. RECOGNITION OF TAXONOMICAL RELEVANT PARAMETERS

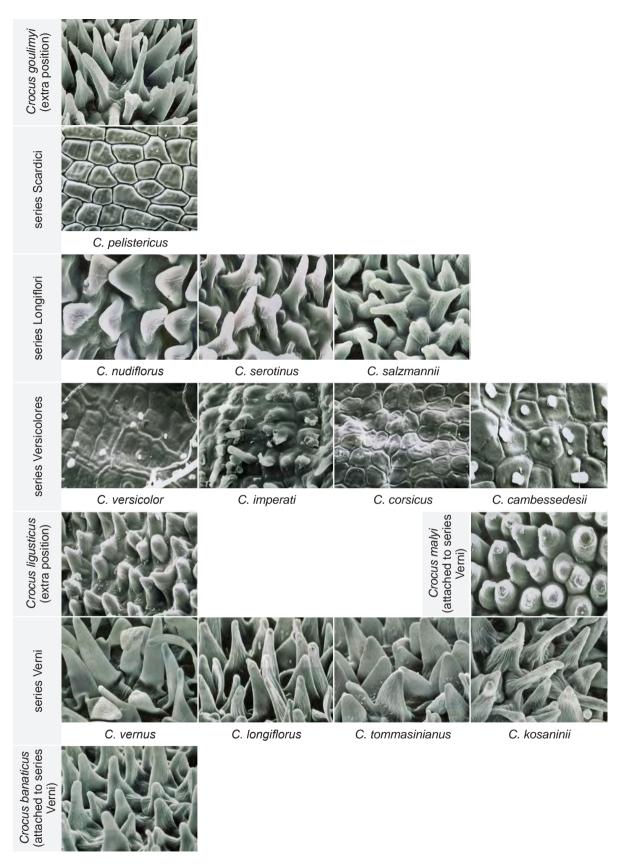
From the taxonomic point of view and dependent on section or series it is useful to consider and/or measure only the most significant parameters for the secure identification of a crocus. In our now more than 30 years lasting work on crocus it became more and more difficult to use only the information of the last important revision of the genus by Mathew (1982) to identify upcoming new taxa. During the years of field research and by getting more and more experience it turned out that some morphological and phenotypic parameters are more useful than others. In the following we present the most appropriate morphological parameters and how they should be measured as well as the more suitable phenotypic characters and what of these have to be recognised.

### 3.1 Morphometry of continuous parameters

As all of the relevant morphological parameters are continuous ones, measurements of randomly selected and of a statistically sufficient number of specimens is necessary to receive reliable results. As we have shown in some of our publications (Kerndorff et al. 2003, 2004b) an information e.g. about the length of filaments of a species is worthless if measured only of a herbarium specimen or of few specimens in a pot as the variability of this and other comparable parameters is in general rather high and can even overlap with the results of other species. In most cases, if the amount of investigated specimens is statistically sufficiently high (in our cases the optimum was around 35 individuals of a population) the distribution of the measurements usually follows a Gauss-curve, better known as "normal distribution". From this normal distribution the median-value, mean-value, percentiles and many other statistical values can be received with a definite probability of being close to the "true" value of the parameter in question. As our measurements e.g. of all our investigated populations show, the mean-values of the continuous parameters and other selected phenotypical parameters are, if used together, very useful to distinguish between the known taxa. What and how it is to be measured or recognised is shown in the following chapters.

### Corm

The dimension (size) of the corm is the only morphometric parameter to be measured in length and width. However, it is in many cases not a useful taxonomic one as it varies not only dependent on the species but greatly on the availability of nutrients in the soil. There are of course exceptions but these can be only recognised if a greater number of corms of one species from different localities is available for measurements, but even so the benefit of those measurements stands in no relation to the effort. Typical and constant extreme differences can be seen e.g. with corms of species of series *Scardici* which are very small (5-8 mm in diameter) and series *Crocus* which are rather large (up to 25 mm, in cultivated specimens even up to 35 mm in diameter). In case a taxon has to be newly described, the corm size may be mentioned even when it has obviously not an outstanding dimension.



 $\textbf{Fig. 24}: \ \ \textbf{Variability of testa micro-structure of species belonging to section Crocus}^1.$ 

<sup>1</sup>according to the phylogenetic results of HARPKE et al. (2013).

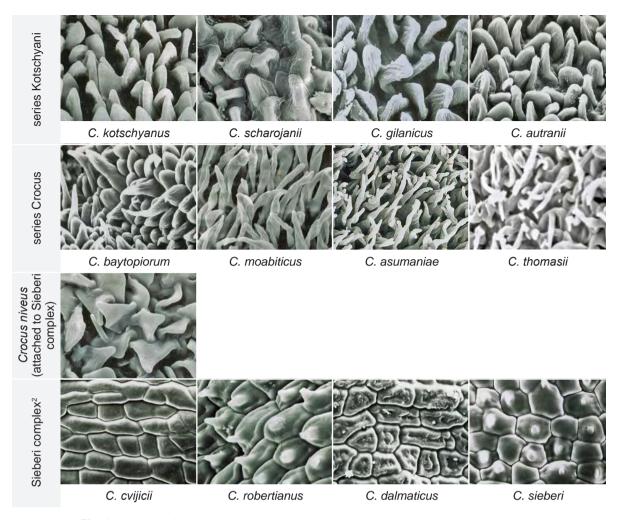


Fig. 24: continued.

<sup>1</sup>according to the phylogenetic results of HARPKE et al. (2013).

### **Corm tunic**

Unlike to other genera of the *Iridaceae*, e.g. *Gladiolus*, the corm tunic of crocuses is much more distinct and in fact different even from series to series and in several cases also different from species to species. There is, however, only a comparatively low number of parameters which are worth to be measured (Fig. 25). Most of the relevant characters of the corm tunic are phenotypic and dealt with in chapter 3.2.

### Cataphylls

For cataphylls there is no useful continuous parameter to be measured.

### Prophyll, bract, bracteole

For these leaves there are no useful continuous parameters to be measured. The main reason for this is that the plant has to be dissected which is not recommended due to the protection of individuals and species.

### True leaves

The only continuous parameters worth measuring in case of the true leaves are their width at flowering time at their broadest position and the width of the white stripe in relation to the leaf-diameter (Fig. 26). It can be very small like in *C. banaticus* or *C. striatulus* (<1/5 of leaf diameter) or very conspicuous like in *C. artvinensis* (>1/3 of leaf-diameter). The length of the leaves is taxonomically little informative as they are continuously growing during the season and have different lengths at different times. In some species they are shorter than the flower at flowering time but can reach up to 60 cm in mature plants.

### Segments

The size of the flower is certainly a relevant taxonomical parameter as can be seen comparing different *Crocus* species like *C. salzmannii* and *C. danfordiae*. One should measure the length and the width of at least 20 randomly selected individuals. The measurements can be done only for the outer segments as these

<sup>&</sup>lt;sup>2</sup>this series has to be newly defined in a revision of the genus

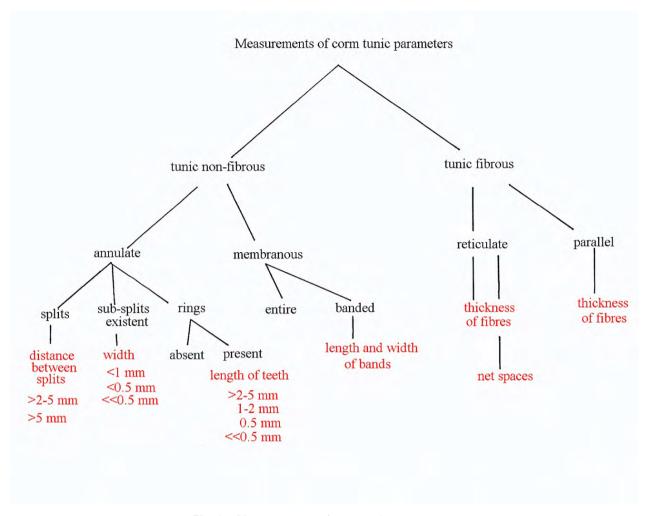


Fig. 25: Measurements of corm tunic parameters.

are always in proportion to the inner ones (Fig. 27). The proportion of the mean length to the mean width of segments is a useful parameter for the type of flower. Values from 2-2.5 signalise a bowl-shaped flower, values from 2.5-3.5 stand for the "normal" Crocus-flower and values from 3.5-5 signalise a more or less starry star-like flower.

### Tube and throat

There are no useful continuous parameters to be measured.

### **Filaments**

The only continuous parameter in this case is the length of the filaments. It should be measured as it is shown in Fig. 28.

### **Anthers**

The only continuous parameter in this case is the length of the anthers. It should be measured as it is shown in Fig. 29.

### **Styles**

The only useful continuous parameter in this case is the length of the style-branches. It should be measured as it is shown in Fig.30. Another parameter with some significance for taxonomy that should be mentioned here is the length of the styles according to the stamen. They can be longer, equal or shorter. To receive adequate values it is necessary to investigate at least 20 individuals of a population (Fig. 31). For example: of twenty investigated specimens of a population 11 have styles significantly longer as stamens, 5 are equal to the length of stamen and 4 are shorter than stamen. This means the majority (16) or 80% of the population has styles longer to equal the stamens and 20% has shorter ones. This parameter can also be coded as follows: longer is set +1, equal is set 0, and shorter is set -1. If one adds the proportions for all 20 individuals the result is as follows (11x + 1) + (5x 0) + (4x - 1) / 20 = +0.35 There can be of course only numbers between -1 and +1 but they give a good impression about the actual situation in a population and what is even more important the result can be used statistically in this form.

length of anthers

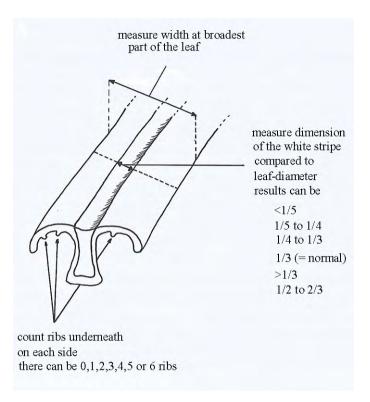


Fig. 26: Measurements and counts of true leaves parameters.

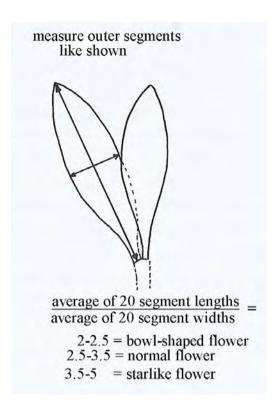


Fig. 27: Measurements of segments.

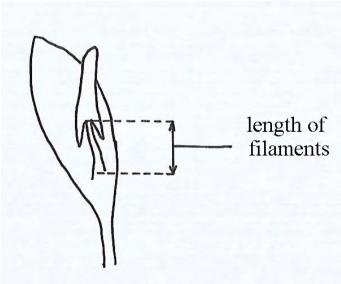


Fig. 28: Measurement of filament length.

Fig. 29: Measurement of anther length.

### **Capsules**

The capsules vary too much in their sizes (length and width, see Fig. 22) dependent on nutrients in the soil and climatic conditions which can be different even from season to season. Therefore they are not of great taxonomical value.

### Seeds

The only relevant parameters of seeds which can be measured are their sizes (length and width, Fig. 32) although the taxonomical value of this parameter is comparatively limited like with the capsules and should be used only in connection with other ones.

### 3.2 Recognition of phenotypic characteristics

### Corm

A rather significant phenotypic parameter of the corm seems to be the shape as can be seen from the examples in Fig. 5. Unfortunately these are rather idealised and because of endless transitional forms which occur in the genus it is difficult to determine exactly a special corm shape. The quote of misidentifications using this parameter alone would be high so it has only a limited value for taxonomy and is only useful in combination with other parameters.

### Corm tunic

The corm tunics of crocuses vary greatly and belong certainly to one of the most relevant parameters for identification of species. There are many phenotypic parameters connected to them and should be considered like done by us when creating the determination key based on major corm tunic characteristics. Relevant are their condition (coriaceous or membranous) splits, rings, teeth on rings, necks, parallel bands, reticulate, parallel or combined fibres in different levels of the tunic, caps, and bottom plates. For details we refer to Fig. 8.

### Cataphylls

For the cataphylls also a number of characteristics are taxonomically relevant like their colour which can be silvery (most frequent), brownish or with brownish or green tips, yellow or green with green veins. They can last for only one season and be permanently silvery-white or getting brown with age or they persist as dark brown reminders for more than one season (for more details see chapter 2.4 (Fig. 15).

### Prophyll, bract, and bracteole

From the taxonomical viewpoint the most important parameter of these leaves is their presence or absence which should be determined in any new description. Less important are shapes or colours although they can be decisive in some cases. Most of these leaves are colourless/silvery and skinny, they can get brown with age but they are never persistent (Fig. 33).

### **True leaves**

According to their homology to the tunics they show a comparable diversity to these. Taxonomically relevant are the numbers of leaves per scape of mature (flowering) plants; the co-

lour of leaves (chapter 2.6), their longitudinal shapes (Fig. 34), the shape of cross-section (Fig. 17) and number of ribs in the grooves underneath (Fig. 26), hair on leaves which can be thinly distributed all-over or only at the leaf-edges (ciliate). Taxonomically less important seems to be the development of leaves at anthesis as it is greatly influenced by climatic factors and growing heights. In some populations at the same locality we could observe the whole range of leaf-development from just visible to overtopping the flower.

### **Segments**

As the shapes and tips of segments show endless variations even inside a population (Fig. 18) the taxonomical value of this parameter is rather restricted. To find out if a segment shape is taxonomical relevant it must be a more or less constant feature of a species like this is the case for the acuminate segments of C. vallicola. To proof the relevance of a taxon an adequate investigation of a population is necessary. Unfortunately, a greater part of the crocus species does not have constant shapes of their segments. This makes this parameter unsuitable for taxonomic purposes in many cases. Similar can be said for the basic colour of species which is everything but constant as we could proof in hundreds of investigated populations. This makes a comparison with standard colours obsolete. The most prominent markings on the outsides of the outer segments fall also under this category. This parameter is even more subtle than the colours and withdraws itself from a systematic approach. The only possibility to handle this problem is a detailed description of these markings as far as possible. Then, compared with other detailed descriptions differences of taxa may be revealed by these parameters. A yet rarely recognised but very helpful and not to be neglected parameter of the segments originates by their three-fold cell-layer. These can be differently pigmented and marked which makes it useful to recognise the differences between the layers especially of the outer and inner ones. An effect of differently pigmented layers is e.g. that the insides of the inner segments are merely uniformly coloured or that the throat is yellow even when the outside (= perianth tube) is brownish-violet.

### **Tube and throat**

There are three taxonomical useful parameters to be recognised, the colour of the throat (inside layer of the segment), the colour of the perianth tube at the apex (outside layer of the segment), and the presence or absence of "hair" in the throat. The throat as well as the apex of the perianth tube can be very differently coloured as is shown in Fig. 19 and are in many cases rather constant within a species which means they are of taxonomical relevance.

### **Filaments**

Three phenotypic parameters of the filaments have taxonomical relevance because they are widely constant in contrary to other parameters of the perianth. This is at first the colour which varies from colourless to shades of yellow and orange to deep brownish-violet or purple but is rather constant in a population (Fig. 20). Secondly there are different attachments of the filaments to the anthers. The attachment can be either rather broad which results in a stiff immobile position of the whole stamen or is a thin string-like connection to the anthers which gives them the flexibility to bend in two directions in case pollinating in-

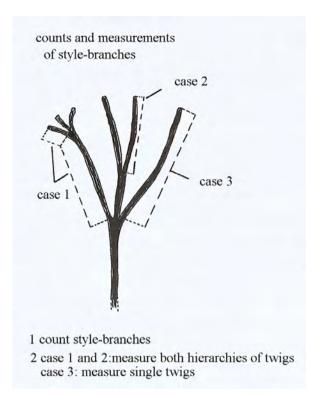


Fig. 30: Counts and measurements of style-branches.

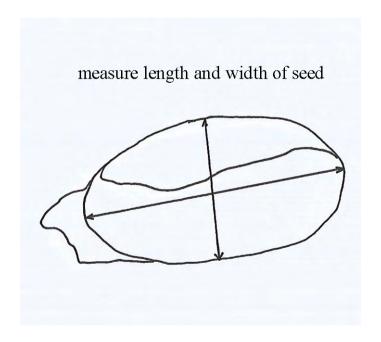


Fig. 32: Dimension of seeds.

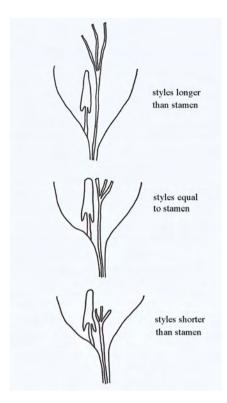


Fig. 31: Proportion of stamen to style.

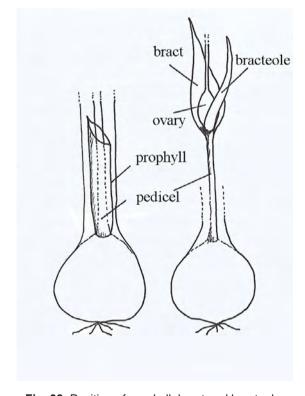


Fig. 33: Position of prophyll, bract and bracteole.

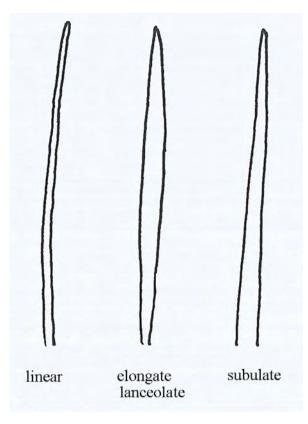


Fig. 34: Main leaf-forms of Crocus.



Fig. 35: Spread style-branches of C. vernus.

sects touch them. It is obviously a trick of nature for a more successful pollination. Third the base of the filaments can be hairy or glabrous which was in the history of the genus a much more important parameter for taxa differentiation as it is nowadays.

### Anthers, thecae, connectives, and pollen

Anthers of crocuses can be morphologically and phenotypically very different from species to species as is shown in Fig. 20. This is true for the main types of colours of the theca (yellow, white, or black) which are of taxonomic relevance as comparisons with genetic results show. The shape of the anthers of a species is comparatively constant and always arrow-shaped. The arrow can have very long or rather short and nearly obtuse lobes. The connectives can be narrow or broad and have different colours too. These are, as mostly constant, also of taxonomical relevance. Although only existent in one species (*C. banaticus*) the anthers can be extrorsely orientated. In contrary to that the colour of the pollen has very little taxonomical value.

### **Styles**

The styles of crocuses show a wide spectrum of variety concerning colours and division (Fig. 21). Because of this both parameters seem to have taxonomical potential as they are really extreme in some species. Unfortunately the clear divisions as shown in Maws plate (Fig. 21) are far away from being constant for a population or even for a species and one can find all kind

of transitional forms. So, before using these parameters for determination a wide range of specimens has to be investigated in a population. The kind of divisions, the number and length of the resulting branches (Fig. 21) can be relevant characters if investigated of a statistically relevant number of specimens (Fig. 30). Contrary to the present knowledge no entire styles exist with *Crocus*, instead, all species have primarily a division into three branches. This can be rather indistinct when sub-divisions occur already in the lower part of the style ending in a bunch of branches like with C. banaticus or when branches have fan-shaped or trumpet-like endings tightly pressed together like in types of C. vernus. If one spreads the style of C. vernus the three branches are immediately visible (Fig. 35). Another parameter of relevance can be the ends of the style-branches if investigated in an appropriate number of individuals of a population. There are either ends with just a vertically pronged margin or conspicuously expanded ends which can have different forms between fan-like or trumpet-shaped. A parameter, although interesting, can be observed well only in dried specimens using a stereo-microscope or 20-fold magnification glass are papillae on the branches which can be glabrous, scabrid or papillous.

### Capsules

The capsules are only of limited taxonomical value as the few parameters (size, form and shape of the apex) have in many cases little significant differences. These parameters are only useful to characterise some series and new taxa.

### Seeds

Taxonomically relevant phenotypic parameters of seeds are their shapes, colours, raphes and caruncles (Fig. 23). The latter ones are in general good visible if developed which is dependent on species. For a better and more precise observation of these parameters it is advisable to use a magnification glass of (10)-20 fold magnification. One soon will find out that the variation of shapes, raphes and caruncles in crocus seeds is unique. Also, almost all kinds of colours are existent e.g. shades of beige and brown but also red, black, bronze and green colours occur at least in fresh seeds as colours can change dramatically with age. Comparable are forms of seeds the developed raphes and caruncles.

### CONCLUSIONS AND RECOMMENDATIONS

The major conclusion of this work is that a largely mistakefree identification of *Crocus* species is only possible using as many relevant parameters as possible. The following are of taxonomic value and are recommended for measurements, counting or recognition for species determination:

### Morphometric parameters (17)

### Corm tunic (6)

- annulate: distance between splits, dimension of sub-splits if present, length of teeth on rings if present.
- membranous: length and widths of bands
- fibrous: reticulate: thickness of fibres, dimension of net spaces parallel: thickness of fibres

### True leaves (3)

- width at the broadest part of flowering specimens
- width of the white stripe according to leaf-diameter
- · number of ribs underneath

### Segments (3)

- Length of outer segments
- Width of outer segments
- Proportion of length to width of 20 specimens

### Filaments (1)

· Length of filaments

### Anthers (1)

Length of anthers

### Styles (1)

Length of style-branches

### Seeds (2)

length and width of seeds

### Phenotypic parameters (44)

### Corm tunic (9)

- annulate: condition, splits, rings (absent/present), teeth on rings (absent/present), necks
- membranous: shape of bands
- fibrous: reticulate, parallel or combined fibres at different levels of main tunic, shape pf caps and bottom plates

### Cataphylls (2)

· colour and persistency

### Prophyll (1)

absent/present

### Bract & bracteole (3)

absent/present, conspicuous/not conspicuous, colour

### True leaves (6)

 number per scape, colour, longitudinal shape, shape of crosssection, number of ribs underneath, hair

### Segments (2)

 detailed description of colour-ranges and markings especially towards perianth tube

### Tube (1)

colour and markings near apex

### Throat (4)

colour and dimension, hair (absent/present), absence/presence
of a different colour in the deeper throat, absence/presence of a
different coloured corona above the throat

### Filaments (3)

 colour, shape of attachment to the anther, absence/presence of hair at base

### Anthers (theca, connective) (3)

colour, shape of arrows, position (introrse/extrorse)

### Styles (4)

 colour, division (including different hierarchic levels), shape of end of branches, papillae

### Capsules (2)

shape, shape at apex (cute, acuminate, obtuse etc.)

### Seeds (4)

Shape, colour, development of raphe and caruncle

As we could proof in several publications (Kerndorff et al., 2011, 2012, 2013) the above listed 17 morphometric and 44 phenotypic parameters are the most useful ones for a distinct description of a crocus without greater overlaps to other taxa. This is very important as many taxa of section *Nudiscapus* can be rather similar and only a detailed characterisation allows their differentiation. As our experience shows it is possible to select for different series individually optimized sets using the parame-

ters above. This means not for every determination of a crocus the entire set of all parameters is necessary. But, on the other hand, it is difficult for unexperienced people to decide which parameters have priority for which series! Furthermore, the majority of these parameters is needed to establish reliable determination keys for the revision of the genus.

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